

*Miconia amilcariana* (Melastomataceae: Miconieae), a New Species from the Venezuelan Andes with Notes on the Distribution and Origin of Dioecy in the Melastomataceae

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*Miconia amilcariana*, known only from the Cordillera de Trujillo in the Venezuelan Andes, is described, illustrated, and compared with its presumed closest relatives in *Miconia* section *Cremanium*. This new species is distinguished by its 5-merous unisexual flowers that are produced on different individuals (dioecy), 3-locular ovary, 5–7-plinerved leaf blades, and indument on internodes, inflorescences, and abaxial foliar surfaces that consists of a mixture of stellate and asperous-headed hairs. A list of the known dioecious species of *Miconia* is provided together with comments on the geographical distribution and probable origin of dioecy in the Melastomataceae.

Resumen

*Miconia amilcariana*, conocida únicamente de la Cordillera de Trujillo en los Andes Venezolanos, es descrita, ilustrada, y comparada con sus presuntos parientes más cercanos en *Miconia* sección *Cremanium*. Esta nueva especie se distingue por sus flores unisexuales, 5-meras, que se producen en individuos separados (dioecismo), ovario 3-locular, laminas foliares 5–7-plinervadas, e indumento en los entrenudos, inflorescencias, y superficie foliar abaxial que consiste de una mezcla de tricomas estrellados y tricomas de cabeza áspera. Se incluye una lista de especies dioicas conocidas de *Miconia* con comentarios sobre la distribución geográfica y posible origen del dioecismo en las Melastomatáceas.

The late John J. Wurdack (1921–1998) identified many of the Melastomataceae collected during exploration of the flora of Guaramacal National Park (Portuguesa and Trujillo states) and neighboring areas in the Venezuelan Andes. In doing so he recognized the following as representing an undescribed species of *Miconia* Ruiz & Pav., but for a variety of reasons he did not work up the available material for publication. We do so here with profound appreciation for the many contributions John made to our understanding of not only Melastomataceae, but also Venezuelan botany.

SPECIES DESCRIPTION

*Miconia amilcariana* Almeda & Dorr, sp. nov.

TYPE.— VENEZUELA: Trujillo: Mpio. Boconó, El Campamento-Pele Ojo, bajando hacia Quebrada Honda. 1900–2120 m, 9–16 July 1998, *B. Stergios* 17582 (holotype, PORT!; isotypes, CAS!, US!). Figure 1.

Section *Cremanium*. Frutex vel arbor (1.5)2–10 m; ramuli primum obtuse sulcato-quadrangulati demum teretes sicut inflorescentia venae primariae et secundariae subtus pilis asperis et pilis stellati induti. Lamina 10.5–25 × 4–12 cm, elliptica vel oblongo-ovata vel ovata apice acuminata basi rotundata vel cordata, 5–7-plinervata, supra glabra. Panicula 6.5–12 cm multiflora; flores 5-meri, bracteolis 0.5 × 0.25 mm subulatis mox deciduis. Hypanthium (ad torum) 1 mm longum; calycis tubus non evolutus lobis interioribus 0.25 × 0.25 mm dentibus exterioribus minutis ca. 0.3 mm eminentibus. Flores masculini: stamina isomorphica glabra; filamenta 1.5–1.6 mm longa; thecae 0.5 × 0.5 mm obovato-oblongae late quadriporsae et 4-loculares; ovarium abortivum. Flores feminei: stamina abortiva, filamentis 0.5 mm longis, thecis ca. 0.4 mm longis; stigma peltatum; stylus 1–1.2 × 0.2 mm glaber; ovarium 3-loculare et  $\frac{3}{4}$  inferum, apice glabro.

Trees or understory shrubs (1.5)2–10 m tall with obtusely sulcate-quadrangular internodes that become terete with age. Uppermost cauline internodes, juvenile unexpanded leaves, and inflorescence rachis copiously but deciduously covered with a pale tan mixture of sessile-stellate and stalked-stellate and asperous-headed hairs. Leaves of a pair equal to subequal in size; petioles (1.7)2.5–7.5 cm long; blades 10.5–25 × 4–12 cm, elliptic, oblong-ovate to ovate, apex acuminate, base broadly rounded to nearly cordate, margin mostly entire but varying to crenate-serrulate or denticulate, 5-plinerved, the innermost pair of primary veins diverging from the median vein 2–10 mm above the blade base, adaxially ± glabrous at maturity, abaxially covered with a sparse to copious indument of sessile-stellate, stalked-stellate and asperous-headed hairs mostly on the primary and higher order veins with an inconspicuous scattering of minute orange-brown glands on the higher order veins and the actual blade surface. Inflorescence a terminal multiflowered panicle 6.5–12 cm long; bracteoles linear-subulate, 0.5 mm long and more or less 0.25 mm wide, glabrous, early deciduous and typically absent at anthesis. Flowers 5-merous and unisexual on pedicels 0.5 mm long, covered with a scattering of rusty-brown glands. Hypanthia (at anthesis) 1 mm long to the torus, glabrous or with a few minute rusty-brown glands. Calyx tube obsolete, the calyx lobes 0.25 × 0.25 mm, glabrous, bluntly rounded-triangular, exterior teeth 5, thickened and ± triangular or obconic, ca. 0.3 mm long but not projecting beyond the calyx lobes; torus glabrous on the abaxial side. Petals 1–1.1 × 0.5–0.6 mm, white, glabrous, obovate and ± concave, sometimes deeply notched or hooked apically in staminate flowers. Anthers white, isomorphic, cuneiform or obovoid, widest at the apex, 4-celled and 4-pored, the filaments 1.5–1.6 mm long, anthers 0.5 mm long and ca. 0.5 mm wide apically in staminate flowers, the filaments ca. 0.5 mm long, non-polleniferous and collapsed anthers ca. 0.4 mm long in pistillate flowers; connective prolonged 0.25 mm below the thecae in staminate flowers but neither elevated nor appendaged. Ovary (in fruit)  $\frac{3}{4}$ -inferior, 3-locular, the apex glabrous. Style straight, glabrous, 1–1.2 mm long, stigma peltate in pistillate flowers, these structures vestigial and barely evident in staminate flowers. Berry 2–2.5 × 2.5–3 mm, globose, green flushed with pink when immature becoming bluish or purple-pink at maturity. Seeds 0.5–0.75 mm long, ovoid to ovoid-pyramidate, the testa irregularly granulate.

**DISTRIBUTION, HABITAT AND PHENOLOGY.**— This species grows in openings created by roads and other clearings in lower montane and montane (cloud) forest in the Cordillera de Trujillo, the northeastern-most range of the Venezuelan Andes at 1,700–2,550 m (Fig. 2). Flowering and fruiting specimens have been collected in July and from September through January.

**PARATYPES.**— **VENEZUELA:** Lara: Mpio. Moran, Carretera desde Humacaro Alto hacia Guaito, 2,200 m, 14 Nov. 1984, *van der Werff & Rivero* 7919, ♀ (US). **Portuguesa:** Mpio. Sucre, La Divisoria de la Concepción, 9°18'N, 70°06'W, 1,700 m, 23 Oct. 1985, *van der Werff et al.* 7552, ♂ (PORT). **Trujillo:** Mpio. Boconó, Parque Nacional Guaramacal, vertiente norte (9°14'59"N, 70°12'43"W), 2,100 m, 17–18 Jun. 1995, *Cuello et al.* 999, ♀ (CAS, COL, MO, PORT, US). *Ibid.* (9°14'48"N, 70°12'15"W), 2,400 m, 1–3 July 1995, *Cuello et al.* 1077, ♂ (MO, PORT, US). *Ibid.* (9°14'38"N, 70°13'12"W), 1,850 m, 15–16 July 1995, *Cuello et*

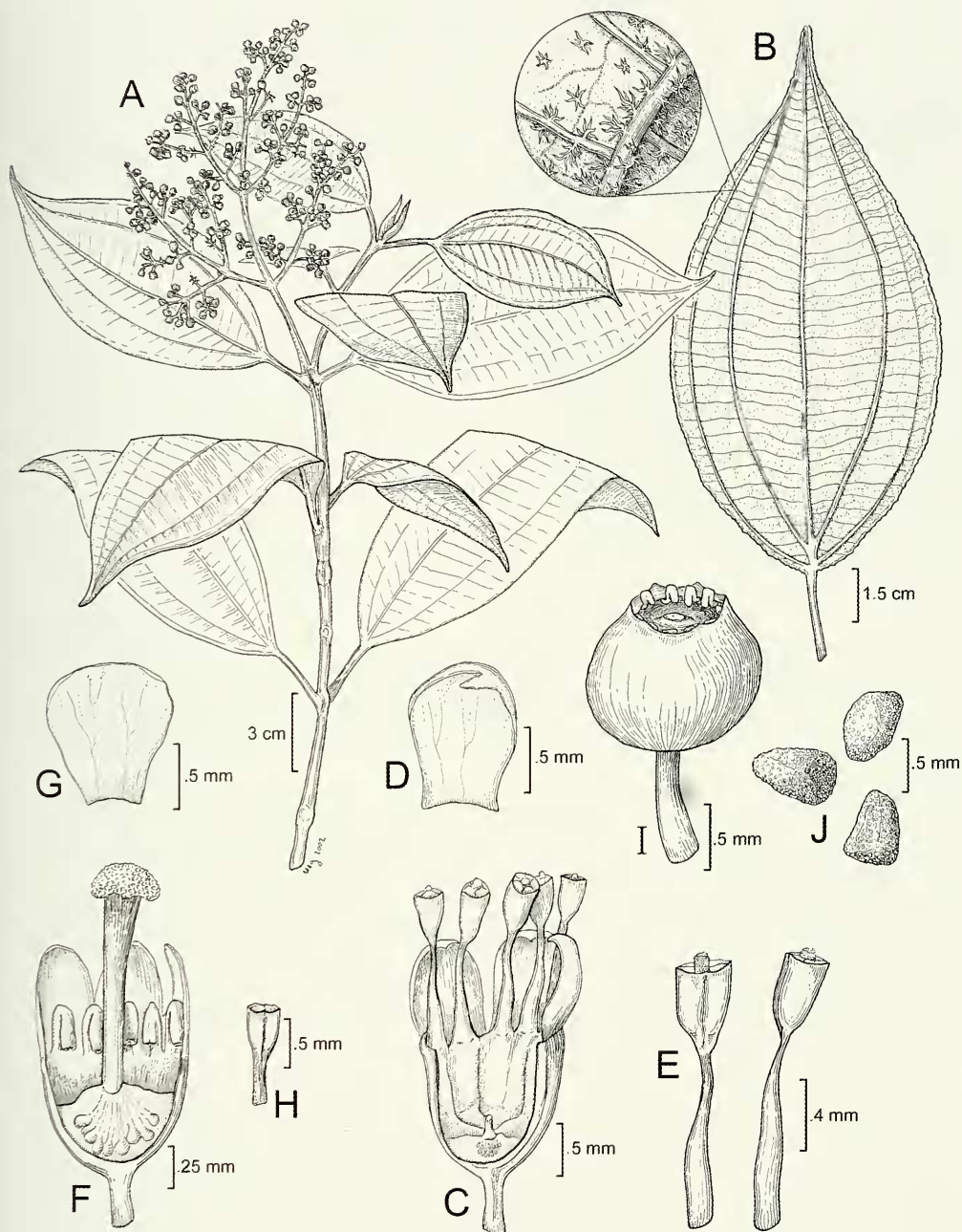


FIGURE 1. *Miconia amilcariana* Almeda & Dorr. A. habit; B. representative leaf (abaxial surface) with enlargement showing indument; C. staminate flower (longitudinal section) showing stamens and vestigial style; D. petal (staminate flower) showing notched apex; E. stamens from a staminate flower showing protruding septum; F. pistillate flower (longitudinal section) showing style, stigma, and vestigial stamens; G. petal (pistillate flower) showing rounded apex; H. vestigial stamen (pistillate flower); I. berry; J. seeds. (A, B, I and J from *Stergios 19115*; C-E from *Tillett 739-614*; F-H from *Dorr & Barnett 7529*.)

*al.* 1185 (PORT); Parque Nacional Guaramacal, vertiente sur, ca. 9°12'45"N, 70°09'51"W, 2,300 m, 3–5 Jan. 1996, *Cuello et al.* 1327, ♀ (CAS, K, PORT, US, VEN); Montañas de Misisi, carretera vieja Trujillo-Boconó (ca. 9°21'N, 70°18–19'W), ca. 12 km by air NW of Boconó, 2,000–2,400 m, 31 Oct. 1990, *Dorr & Barnett* 7529, ♂ (NY, PORT, US), *Ibid.*, 31 Oct. 1990, *Dorr & Barnett* 7550, ♀ (NY, PORT, US, VEN), *Ibid.*, 1 Nov. 1990, *Dorr & Barnett* 7570, ♀ (NY, PORT, US, VEN), *Ibid.*, 1 Nov. 1990, *Dorr & Barnett* 7572, ♂ (NY, PORT, US, VEN); Parque Nacional Guaramacal, between Cerro El Diablo and Qda. Honda, ca. 11 km S of Boconó on road from Fundación La Salle to El Santuario (9°09'N, 70°17'W), ca. 2,100 m, 21 July 1995, *Dorr et al.* 8219, ♂ (CAS, PORT, US); Parque Nacional Guaramacal, trail from la Laguna de las Aguas Negras to la Qda. Salvaje, N slope, 9°19'N, 70°11'W, 27 Oct. 1998, *Dorr et al.* 8281, ♀ (AAU, CAS, PORT, US); Parque Nacional Guaramacal, road from Boconó to Guaramacal, SE of Boconó, ca. 15 km from the post of the park guards, S slope, 9°13'N, 70°12'W, 2 Nov. 1998, *Dorr et al.* 8416 (CAS-♂, CTES-♀, F-♀, NY-♀, PORT, US-♀); Parque Nacional Guaramacal, sector vertiente norte, carretera al Páramo Guaramacal, 2,100–2,550 m, Jan. 2000, *Stergios* 19115 (PORT, US), *Ibid.*, *Stergios* 19123, ♀ (PORT, US); Parque Nacional Guaramacal, sector quebrada Honda-Pele Ojo, El Santuario, 1,950–2,100 m, Jan. 2001, *Stergios & Caracas* 18986, ♂ (CAS, PORT, US-♀); Parque Nacional Guaramacal, vertiente norte, camino Laguna de los Cedros-cresta del páramo, 9°07'N, 70°16'W, Jan. 1991, *Stergios & Palacios* 18690, ♀ (PORT, US); Cerro Guaramacal, Boconó, bajando hacia el caserío de Guaramacal, 25–26 Nov. 1982, *Stergios et al.* 4746, ♂ (PORT, US); Parque Nacional Guaramacal, sector quebrada Honda de El Santuario, 1,880–2,000 m (UTM: 1012298N, 359185E), Nov. 2001, *Stergios et al.* 19365, bud (PORT, US); 4–5 km along old Boconó-Trujillo road, from crossroad with new highway at 2 km S of lateral to Burbusay, ca. 2,400 m, 6 Sep. 1973, *Tillett* 739-614, ♂ (US).

**DISCUSSION.**—Based on its obovoid-oblong anthers with a wide 4-pored apex and protruding septum, *Miconia amilcariana* is assigned to section *Cremanium* (D. Don) Naudin, the largest (with some 214 species) of the 10 currently recognized sections of *Miconia*. The distinctive features of *M. amilcariana* include its 5-merous unisexual flowers that are produced on different individuals (dioecy), anther pores that are essentially truncate or slightly inclined ventrally at the apex, peltate stigma on pistillate flowers, 3-locular ovary, 5–7-plinerved leaf blades, and indument on internodes and abaxial foliar surfaces that consists of a mixture of sessile- and stalked-stellate hairs, and asperous-headed hairs.

Among the species of section *Cremanium*, *Miconia amilcariana* is most similar to *M. laetevirens* L. Uribe of Colombia and *M. tabayensis* Wurdack of Venezuela. The former differs from the new species in having hermaphroditic flowers, 3-nerved or shortly 3-plinerved leaf blades, elliptic to obovate-spatulate bracteoles that are persistent, and a clavate-truncate to subcapitate stigma. The anthers of both *M. laetevirens* and *M. amilcariana* are similar in shape and in being 4-loculed and 4-pored but the former differs in having the two dorsal anther sacs positioned above (superposed) the two ventral anther sacs with all the apical pores conspicuously inclined ventrally to give the overall anther a somewhat curved aspect (see Uribe Uribe 1966). In *M. amilcariana* all the locules of each anther diverge from the same basal position to give the anther a straight posture.

In overall morphological similarities, *Miconia amilcariana* appears to be most closely related to *M. tabayensis*, another dioecious species (Wurdack 1973). The latter has leaf apices that are shortly obtuse-acuminate (vs. acuminate to long-acuminate), leaf bases that are obtuse to rounded (vs. broadly rounded to nearly cordate), and linear-oblong bracteoles that are 0.7–1 mm long (vs. linear-subulate bracteoles that are 0.5 mm long). The most striking feature of *M. tabayensis* that readily distinguishes it from *M. amilcariana* is the indument on branchlet internodes, the inflorescence, and abaxial foliar surfaces. This indument, which is fairly dense and persistent, consists of inconspicuously septate simple hairs 0.5–1.2 mm long that are somewhat crisped and often forked or barbed distally. In *M. amilcariana*, the indument which can be sparse to copious but tardily deciduous consists of a mixture of sessile- and stalked-stellate hairs intermixed with asperous-headed hairs, all of which are prevailing less than 0.5 mm in length. Each species also appears to occur in a different region of montane Venezuela. *Miconia amilcariana* is known from several collections

made in the northeastern-most range of the Venezuelan Andes at 1,700–2,550 m. *Miconia tabayensis*, also endemic to the Venezuelan Andes, has been collected only a few times above Mérida and in a region of the Cordillera de Mérida further south and west near Pueblo El Cobre at 2,300–2,800 m.

The unisexual flowers of *Miconia amilcariana* consistently have vestigial organs of the other sex (Fig. 1F and 1H; Fig. 1C). This is common for dioecious species in families that are largely hermaphroditic like the Melastomataceae. Nectar is typically the attractant in female flowers of dioecious species (Proctor et al. 1996) but sterile anthers may be the prime attractant in female flowers where pollen is the prime reward. This is likely the case in small-flowered species like *Miconia* section *Cremanium* that are probably visited by generalist pollinators.

Although bisexual (hermaphroditic) flowers are the predominant form of sex expression in the angiosperms, dioecy occurs in a wide range of flowering plant families (Endress 1994; Grant 1975; Yampolsky and Yampolsky 1922). According to recent estimates, dioecy occurs in about 7–10% of the world's flora (Allem 2004; Proctor et al. 1996). It is common in isolated insular floras, shrubs of the Mediterranean region, and in nearly 25% of rain forest trees (Proctor et al. 1996). Generalizations on the advantages of dioecy continue to be debated (Allem 2004) since each species or group of species has undoubtedly responded to different selective pressures (Bawa, 1980; Proctor et al., 1996). The long-held hypothesis that the evolution of dioecy has led to the optimization of outbreeding is increasingly questioned since the evidence for an association between dioecy and agamospermy is mounting (Allem 2004). Agamospermy is known or suspected in hermaphroditic species of *Miconia* and related genera (Almeda 2003; Almeda and Chuang 1992; Goldenberg and Shepherd 1998; Renner 1989) but, as yet, we have no definitive information about reproductive biology of the dioecious species of *Miconia*, many of which are still little-collected and poorly known.

Among the approximately 172 genera of Melastomataceae, true dioecism is known only in *Miconia*, a neotropical genus with over 1,050 recognized species. According to our preliminary list (see Appendix I) there are 37 dioecious species of *Miconia* (including 42 taxa). Thirty-two of these taxa occur only in the Andes of South America and 23 of them are restricted to or have geographic ranges including Peru. Additionally, all of the dioecious species are in section *Cremanium* except *M. stenophylla*, which has recently been placed in section *Chaenopleura* (DC.) Triana by Wurdack (1980). Sections *Cremanium* and *Chaenopleura* have obovate or cuneate anthers but the former has apical pores and the latter dehisces by slits. Both sections are closely related and species placed in the latter have been transferred to the former because the distinctions in stamen morphology are not always clear. In a recent molecular phylogeny of the Miconieae (Michelangeli et al. 2004) the few sampled species in these two sections form a clade which suggests that dioecy in *Miconia* may have

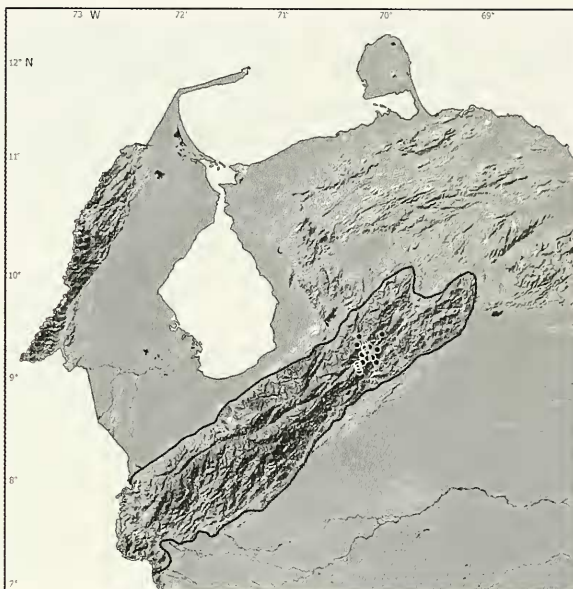


FIGURE 2. Distribution of *Miconia amilcariana* Almeda & Dorr in the Venezuelan Andes; the darker line more or less defining these mountains.

arisen only once. If this is born out by more comprehensive sampling, it also seems possible that dioecy in *Miconia* originated in the South American Andes.

**ETYMOLOGY.**— This species is named for Amilcar Bencomo, Superintendent of Guaramacal National Park. With few tangible resources at his disposal, he has been fiercely protective of the park, an important refuge for Andean flora and fauna and an essential watershed for the people of Barinas, Portuguesa, and Trujillo states. Additionally, he has been an outstanding friend of science and has enthusiastically supported projects that contribute to expanding our knowledge of the natural history of Guaramacal.

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## Appendix I

### The Known Dioecious Taxa of *Miconia* and Their Geographic Distributions

All of these species are placed in section *Cremanium* except *M. stenophylla* which was originally placed in section *Cremanium* but subsequently assigned to section *Chaenopleura* by Wurdack (1980).

- M. milcariana* Almeda & Dorr — Venezuela  
*M. aprica* Gleason — Peru  
*M. boliviensis* Cogn. — Bolivia  
*M. bracteolata* (Bonpl.) DC. — Colombia, Ecuador, Peru {perhaps dioecious, in part, according to Wurdack (1967, 1980)}  
*M. brevistylis* Cogn. — Peru  
*M. caerulea* (D. Don) Naudin ssp. *caerulea* — Peru  
*M. caerulea* (D. Don) Naudin ssp. *vilcabambae* Wurdack — Peru  
*M. choriophylla* Wurdack var. *choriophylla* — Peru  
*M. choriophylla* Wurdack var. *brevifolia* Wurdack — Peru  
*M. clathrantha* Triana ex Cogn. — Ecuador, Peru  
*M. coelestis* (D. Don) Naudin — Bolivia, Peru  
*M. coriacea* (Sw.) DC. — Costa Rica, Dominica, Guadeloupe  
*M. cyanocarpa* Naudin var. *cyanocarpa* — Bolivia, Peru  
*M. dasyclada* Wurdack — Peru  
*M. dielsii* Markgr. — Ecuador, Peru  
*M. dioica* Wurdack — Venezuela  
*M. divergens* Triana — Colombia, Ecuador (poorly known, but probably dioecious as implied by Wurdack, 1980)  
*M. elongata* Cogn. — Bolivia, Peru  
*M. galactantha* Naudin — Peru, Bolivia  
*M. glaberrima* (Schltdl.) Naudin — Belize, Guatemala, Honduras, Mexico  
*M. globuliflora* (Rich.) Cogn. var. *globuliflora* — Martinique, Montserrat, Nevis, St. Lucia  
*M. globuliflora* (Rich.) Cogn. var. *dominicae* R.A. Howard & E.A. Kellogg — Dominica, Montserrat, St. Kitts (incl. Nevis)  
*M. globuliflora* (Rich.) Cogn. var. *vulcanica* (Naudin) R.A. Howard & E.A. Kellogg — Guadeloupe  
*M. henenostigma* Naudin — Guatemala, Mexico  
*M. micropetala* Cogn. — Bolivia, Ecuador, Peru  
*M. minuta* Gleason — Colombia, Ecuador  
*M. oligotricha* (DC.) Naudin — Mexico  
*M. paradisica* Wurdack — Peru  
*M. peruviana* Cogn. — Peru  
*M. polychaeta* Wurdack — Peru  
*M. polygama* Cogn. — Bolivia  
*M. pulverulenta* Ruiz & Pav. — Peru  
*M. purulensis* Donn. Sm. — Guatemala, Honduras, Mexico  
*M. reburrosa* Wurdack — Ecuador  
*M. rubens* (Sw.) Naudin — Colombia, Jamaica, Venezuela  
*M. stenophylla* Wurdack — Ecuador, Peru  
*M. sterilis* Gleason — El Salvador  
*M. tabayensis* Wurdack — Venezuela  
*M. thaminantha* Wurdack ssp. *thaminantha* — Peru  
*M. thaminantha* Wurdack ssp. *huanucensis* Wurdack — Peru  
*M. valida* Cogn. — Bolivia  
*M. vitiflora* J. F. Macbr. — Peru